Adaptive developmental plasticity might not contribute much to the adaptiveness of reproductive strategies. A commentary on M. Del Giudice

Adaptive developmental plasticity might not contribute much to the adaptiveness of reproductive strategies

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A commentary on Del Giudice:
Sex, attachment, and the development of reproductive strategies

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Abstract
Del Giudice's model belongs to those that highlight the role of adaptive developmental plasticity in human reproductive strategies, but at least three other forms of evolutionary adaptation also influence reproductive behavior. Similar to earlier models, the existing evidence suggests that Del Giudice's hypothesized effects are rather weak. In particular, adult attachment styles are hardly predictive of outcomes visible to natural selection.

Del Giudice presents a thoughtful overview, integration, and extension of the now copious literature on what is arguably the most influential developmental hypothesis in modern evolutionary psychology: Children infer environmental risk from cues within their families and adjust their development so that they are well adapted to the reproductive conditions they will face as adults. This is a case of adaptive phenotypic plasticity by conditional development, or *adaptive developmental plasticity*. Theoretically, adaptive developmental plasticity is a perfectly plausible form of evolutionary adaptation (Pigullici, 2005; West-Eberhardt, 2003). However, there are at least three other forms that are equally plausible, and they can all be aligned along a dimension of spatiotemporal environmental stability (Figure 1).

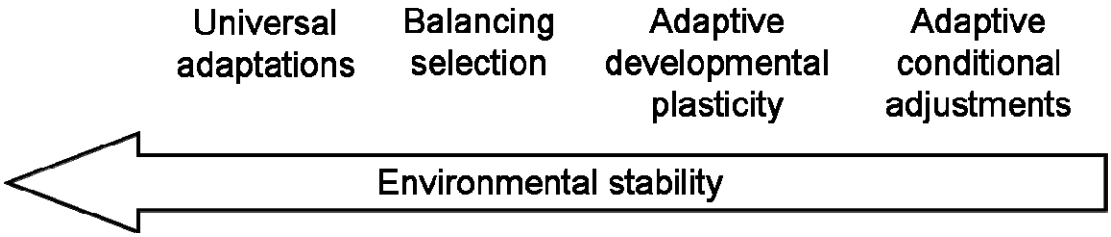

Figure 1. Four forms of evolutionary adaptation. They should be understood as distinguishable points along a continuum, not as distinct categories: Balanced genetic variants can get fixated in the population and thus contribute to evolved adaptations, or they can underlie individual differences in either of the two forms of phenotypic plasticity (Pigullici, 2005; Belsky, 2005), which themselves only differ in how quickly they react to the environment. Which mechanism governs adaptation depends on the spatiotemporal stability of the adaptively relevant environmental features. Different aspects of complex adaptations like life history strategies can be influenced by different mechanisms.

When fitness-relevant environmental features are stable over tens of thousands of years or longer, organisms can evolve *universal adaptations* that reliably develop

every generation (Tooby & Cosmides, 2005). Examples from the domain of human reproductive strategies include the romantic attachment system, which likely evolved in response to the high degree of parental care demanded by human offspring (Fraley, Brumbaugh, & Marks, 2005), and sex differences in the desire for sexual variety, which are basically adaptive so long as women get pregnant and men do not (Schmitt et al., 2003a).

When the environment is less stable and tends to fluctuate, *balancing selection* by environmental heterogeneity can maintain more adaptive genetic variants at higher frequencies in the population (Penke, Denissen, & Miller, 2007a). For example, it has been argued that the phenotypic effects of the seven-repeat allele of the DRD4 polymorphism were more adaptive in societies in which reproductive success is dependent on social competition, whereas the four-repeat allele was likely more advantageous when environmental harshness demanded biparental cooperation (Harpending & Cochran, 2002). A similar logic might hold for the heritable components of traits related to reproductive strategies (e.g. Schaller & Murray, 2008), including the polymorphisms affecting children's sensitivity to rearing environments in Del Giudice's model (Belsky, 2005). However, it will likely not hold for the genetic foundations of the 'K-factor', which is far less plausible from an evolutionary genetic perspective (Penke, Denissen, & Miller, 2007a,b).

Even less stable and more heterogeneous environments favor the evolution of adaptive phenotypic plasticity (Hollander, 2008), which includes developmental plasticity, as discussed by Del Giudice, and much faster *adaptive conditional adjustments* of life history strategies to the current environment. Examples of the latter include adjustments of strategic mating decisions to momentarily faced environmental harshness, quality of available mates, or sex ratio and competition on the local mating market (Gangestad & Simpson, 2000; Penke, Todd, Lenton, & Fasolo, 2007; Lenton, Penke, Todd, & Fasolo, in press). Importantly, romantic attachment styles also show considerable plasticity during adulthood and might even be relationship-specific (Lehnart & Neyer, 2006).

These four different forms of adaptation are not mutually exclusive. I agree with Del Giudice that they will likely all contribute to individual differences in reproductive strategies in a probabilistic manner. However, the critical - and ultimately empirical - question is their relative importance, and this is where I find adaptive developmental plasticity hypotheses of reproductive strategies problematic. When the earlier models that predicted pathways from childhood stress to age of menarche in girls to adult reproductive strategy were empirically tested, hardly any evidence could be found (Ellis, 2004; Hoier, 2003; Neberich, Lehnart, Penke, & Asendorpf, in press). These results led some researchers to retract reproductive strategies altogether and to concentrate on the stress-menarche link (Ellis, 2004).

Del Guidice's model, in contrast, attempts to rescue the causal relationship between childhood stress and adult reproductive strategy by relying much more on attachment styles as the mediating factor and introducing some elegant theoretical refinements, including sex differences and children's attachment styles as disposable phenotypes. However, although there is abundant evidence that adult attachment styles relate to the construal and experience of romantic relationships (Birnbaum et al., 2006; Feeney, 1999), there seems to be surprisingly little evidence that romantic attachment styles actually relate to reproductive strategy-related consequential behavioral outcomes. This is a crucial point, because only consequential behaviors, not subjective experiences, are visible to natural selection and can thus be reasonably explained within an evolutionary framework. To give an example,

sociosexuality shows almost no relationships with attachment styles (Schmitt, 2005a). Strikingly, only restricted sociosexual attitudes, but not sociosexual behaviors, were related to attachment styles in a study by Jackson and Kirkpatrick (2007), but Penke and Asendorpf (in press) showed that attitudes were the only component of sociosexuality not related to a variety of behavioral outcomes, much like self-reported mate preferences are unrelated to actual mate choices (Todd, Penke, Lenton, & Fasolo, 2007). As another example, attachment styles are not predictive of romantic relationship stability once relationship duration is taken into account (Lehnart & Neyer, 2006), and avoidant men and anxious women can have as stable relationships as securely attached people, no matter how satisfied they are with it (Kirkpatrick & Davis, 1994). Even the sex differences in insecure adult attachment styles, which enjoy a prominent role in Del Giudice's model, are in fact quite modest in size (Schmitt et al., 2003b; Schmitt, 2005a) - much smaller than in other mating-related dispositions (e.g. Schmitt et al., 2003a; Schmitt, 2005b). Indeed, it could be argued that their size, even in harsher environments, is too small to be theoretically meaningful (Hyde, 2005).

To conclude, although the available evidence is clearly insufficient to fully evaluate Del Giudice's complex model, it suggests that adaptive developmental plasticity might not account for much variance in reproductive strategies. The theoretical reason for this could be straightforward: During human evolution, environmental changes in reproductive conditions over a few generations were probably less important for successful propagation than changes over much longer or shorter time spans, which lead to universal adaptations, polymorphisms under balancing selection, and adaptive conditional adjustments related to reproductive strategies. Still, I am confident that the myriad of intriguing ideas in Del Giudice's article will inspire future studies, which will hopefully confirm how big or small the contribution of adaptive developmental plasticity to reproductive strategies really is.

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